Oecologia (2008) 157:377–385
DOI 10.1007/s00442-008-1093-z

PHYSIOLOGICAL PHYSIOLOGY - ORIGINAL PAPER

Higher masseter muscle mass in grazing than in browsing ruminants

Marcus Clauss · Reinold R. Hofmann · W. Jürgen Streich · Jörns Fickel · Jürgen Hummel

Received: 11 September 2007 / Accepted: 27 May 2008 / Published online: 9 July 2008

Abstract Using cranioskeletal measurements, several studies have generated evidence that grazing ruminants have a more pronounced mastication apparatus, in terms of muscle insertion areas and protuberances, than browsing ruminants, with the resulting hypothesis that grazers should have larger, heavier chewing muscles than browsers. However, the only investigation of this so far [Axmacher and Hofmann (J Zool 215:463–473, 1988)] did not find differences between ruminant feeding types in the masseter muscle mass of 22 species. Here, we expand the dataset to 48 ruminant species. Regardless of phylogenetic control in the statistical treatment, there was a significant positive correlation of body mass and masseter mass, and also a significant association between percent grass in the natural diet and masseter mass. The results support the concept that ruminant species that ingest more grass have relatively larger masseter muscles, possibly indicating an increased requirement to overcome the resistance of grass forage. The comparative chewing resistance of different forage classes may represent a rewarding field of ecophysiological research.

Keywords Masseter · Phylogeny · Grazer · Browser · Morphology

Communicated by Jean-Michel Gaillard.

M. Clauss (✉)
Clinic for Zoo Animals, Exotic Pets and Wildlife,
Vetsuisse Faculty, University of Zurich,
Winterthurerstrasse 260, 8057 Zurich, Switzerland
e-mail: mclauss@vetclinics.uzh.ch

R. R. Hofmann
Trompeterhaus, 15837 Baruth/Mark, Germany

W. J. Streich · J. Fickel
Leibniz Institute for Zoo and Wildlife Research (IZW),
Alfred-Kowalke-Strasse 17, 10315 Berlin, Germany

J. Hummel
Institute of Animal Science, Animal Nutrition Group,
University of Bonn, Endenicher Allee 15,
53115 Bonn, Germany

Introduction

One of the key assumptions in the investigations of differences between browsing and grazing ungulates is that grasses require greater masticatory forces for a similar degree of functional particle size reduction than browse (e.g. Turnbull 1970; Stöckmann 1979; Solounias and Dawson-Saunders 1988; Clauss et al. 2008). This concept actually did not originate from comparative investigations of plant properties, but from comparative anatomical observations that pointed to a stronger masticatory apparatus in grazing ruminants or ungulates (Turnbull 1970; Ramisch 1978; Stöckmann 1979; Kiplel 1981; Axmacher and Hofmann 1988; Sasaki et al. 2001; Endo et al. 2002). A number of studies have shown that anatomical measurements related to the masticatory muscles, such as osseous muscle insertion areas or canals for nerves supplying the muscles (Solounias and Dawson-Saunders 1988; Janis 1990; Solounias et al. 1995; Solounias and Moelleken 1999; Mendoza et al. 2002; Mendoza and Palmqvist 2006), can help distinguish grazing and browsing ruminants.

However, the only study to directly measure masseter muscle mass in ruminants (Axmacher and Hofmann 1988) found no difference between the feeding types. This study was limited to 22 species examined. Therefore, we assembled a larger data set (48 ruminant species) with more taxonomic groups (giraffidae, cervidae, bovidae) to more

carefully examine the relationship between masseter muscle mass and feeding style.

Materials and methods

Animals were obtained over the years from hunting operations in Germany, Austria, Switzerland, Finland, Canada, Botswana, Namibia and South Africa, and from European zoological gardens. Consistency in method was guaranteed by the fact that the data were mainly generated by one of the authors (R. R. Hofmann), with a few additions by M. Clauss. Additional data were available for two tragulid species (Endo et al. 2002; corrected by one decimal point for an evident typographical error). Body mass was measured directly before dissection of the animals. Each pair of masseters was weighed to ±0.05 g on electronic scales. As the masseter muscle mass in domestic cattle was shown to be independent from the feeding regime (Nakamura et al. 2007), masseter mass data from both free-ranging and captive animals were combined in this study. The average body mass and masseter mass measurements for the individual ruminant species are listed in Table 1.

The unpublished dataset of R. R. Hofmann contains data on more animal species than those given here (cf. Hofmann et al. 2008). However, for a certain subset of animals, body mass had not been determined by weighing, but by using the masseter mass as a surrogate measure, following the suggestion of Axmacher and Hofmann (1988). These data were excluded from the current analysis.

Animals were allocated to feeding type categories [browser (BR), intermediate feeder (IM), grazer (GR)] using the classification of Hofmann (1988), with additional information from more recent publications (Hofmann 1991, 1999; Hofmann et al. 1995). The percentage of grass in the natural diet (%grass) was used to characterize species on a continuous scale; the bulk of the respective data was taken from Van Wieren (1996) and the data collection that formed the basis of Owen-Smith (1997) (data kindly provided by the author), which were supplemented by several other publications (Table 1); whenever seasonal data were available, the %grass used to characterise a species represents the mean of the values from different seasons. These data have been collated using a variety of sources and methods, a problem shared by most comparative analyses performed at the inter-specific level.

Relationships among species were inferred from a phylogenetic tree based on the complete mitochondrial cytochrome *b* gene. Respective DNA sequences were available from GenBank (http://www.ncbi.nlm.nih.gov) for all ruminant species investigated. Sequences were aligned using ClustalX (Thompson et al. 1997), visually controlled and trimmed to identical lengths (1,143 bp). To select the best-fitting nucleotide substitution model for the data, a combination of the software packages Paup* (version 4.b10; Swofford 2002) and Modeltest (version 3.7; Posada and Crandall 1998) was used. Analysis was based on a hierarchical likelihood ratio test approach implemented in Modeltest. The model selected was the general time-reversible (GTR) model (Lanave et al. 1984; Tavaré 1986) with an allowance both for invariant sites (I) and a gamma (G) distribution shape parameter (α) for among-site rate variation (GTR + I + G) (Rodriguez et al. 1990). The nucleotide substitution rate matrix for the GTR + I + G model was likewise calculated using Modeltest. Parameter values for the model selected were: $-\ln L = 15642.5273$, $I = 0.4613$, and $\alpha = 0.8093$ (eight gamma rate categories). The phylogenetic reconstruction based on these parameters was then performed using the maximum likelihood method implemented in TreePuzzle (version 5.2; Schmidt et al. 2002). Support for nodes was assessed by a reliability percentage after 100,000 quartet puzzling steps; only nodes with more than 50% support were retained. The resulting tree is displayed in Fig. 1. The basal polytomy for familial relationships (Bovidae, Cervidae and Giraffidae) was resolved assuming it to be a soft polytomy (Purvis and Garland 1993). In order to meet the input requirements for the phylogenetic analysis implemented in the COMPARE 4.6 program (Martins 2004), we resolved the remaining polytomies to full tree dichotomy by introducing extreme short branch lengths ($l = 0.00001$) at multifurcating nodes. Taxa grouping in the bifurcating process followed the phylogenies proposed by Pitra et al. (2004) for Cervidae and by Fernandez and Vrba (2005) for all other taxa.

The subject of the comparative analyses were individual species, each characterized by its respective mean masseter mass as described above. In order to achieve normal data distribution, both masseter mass and body mass data were ln transformed for all calculations. Following earlier studies (Pérez-Barbería et al. 2001; Clauss et al. 2006; Hofmann et al. 2008), statistical analyses were performed with and without accounting for phylogeny, to test for the validity of a general, functional hypothesis, and to then discriminate between convergent adaptation and adaptation by descent. Linear models were used to compare categorical feeding types (BR, IM, GR) and to investigate the interrelations between body mass, feeding type (as %grass), and masseter mass according to the equation ln (masseter muscle mass) = a+b ln (BM) resp. ln (masseter muscle mass) = a + b ln (BM) + c %grass. In order to additionally include phylogenetic information, we used the phylogenetic generalized least-squares approach (Martins and Hansen 1997; Rohlf 2001) in which a well-developed standard statistical method was extended to enable the inclusion of interdependencies among species due to the evolutionary process. In order to test the robustness of the results, the comparative analysis

Table 1 Number of males (*M*), females (*F*) and individuals of unknown sex (*UK*) investigated for this study and their origin [free-range (*FR*), semi-free-range (*SFR*), zoo (*Z*)], mean (± SD) body mass (kg) and masseter muscle mass (g) measurements of individuals of different ruminant species [of different feeding type: browser (*BR*), intermediate feeder (*IM*), grazer (*GR*)], as well as the percentage of grass in the species' natural diet[a] (*%Grass*) according to literature sources

Species		*n* (M, F, UK)	Origin	Body mass (kg)	Masseter mass (g)	%Grass	Source[b]
Addax nasomaculatus	GR	3, 3, 0	Z	83.8 ± 10.5	262.2 ± 27.3	80	3
Alcelaphus buselaphus	GR	1, 0, 0	FR	217.5	461.0	97	2
Alces alces	BR	1, 1, 4	FR	179.7 ± 56.0	367.0 ± 82.2	2	1
Antidorcas marsupialis	IM	4, 1, 0	FR	43.5 ± 5.6	89.2 ± 9.7	30	4
Antilocapra americana	IM	1, 1, 0	FR	45.0 ± 2.8	86.4 ± 6.4	15	1
Antilope cervicapra	GR	1, 0, 0	SFR	35.0	89.5	75	1
Axis axis	IM	1, 1, 0	SFR	50.5 ± 9.2	94.7 ± 27.8	70	1
Axis porcinus	IM	2, 1, 0	SFR	49.4 ± 13.4	100.6 ± 8.1	50	5
Beatragus hunteri	GR	1, 0, 0	FR	130.0	287.0	90	6
Bos javanicus	GR	0, 1, 0	Z	600.0	996.0	80	est.
Boselaphus tragocamelus	IM	1, 0, 0	SFR	88.0	179.0	60	2
Capra hircus	IM	0, 0, 2	Z	33.5 ± 2.1	76.3 ± 0.2	28	1
Capreolus capreolus	BR	1, 0, 2	FR	26.3 ± 3.2	44.2 ± 11.6	9	1
Cephalophus harveyi	BR	1, 0, 0	FR	8.3	21.8	1	3
Cephalophus monticola	BR	0, 1, 0	FR	4.0	9.2	1	7
Cervus elaphus	IM	1, 0, 0	Z	85.0	177.2	47	1
Cervus nippon	IM	3, 1, 0	FR/SFR	34.8 ± 13.8	64.4 ± 25.0	50	1
Dama dama	IM	2, 5, 0	FR	61.8 ± 19.6	92.8 ± 31.8	46	1
Damaliscus pygarus	GR	1, 0, 0	FR	83.0	196.0	100	9
Elaphurus davidianus	GR	1, 0, 0	SFR	190.6	420.3	75	10
Gazella subgutturosa	IM	1, 0, 0	Z	13.1	25.0	50	11
Giraffa camelopardalis	BR	0, 1, 0	Z	800.0	1026.4	0	2
Hippotragus niger	GR	1, 1, 0	FR	177.5 ± 81.3	358.0 ± 166.9	93	12
Hydropotes inermis	IM	2, 4, 0	SFR	12.7 ± 1.4	26.2 ± 4.4	50	10
Kobus leche	GR	1, 0, 0	Z	72.0	149.2	95	3
Madoqua guentheri	BR	2, 2, 0	FR	4.4 ± 0.2	9.6 ± 1.9	5	14
Mazama americana	BR	3, 3, 0	FR	14.2 ± 5.4	27.5 ± 9.3	1	15
Muntiacus reveesi	BR	0, 0, 2	SFR	12.7 ± 1.6	26.4 ± 1.9	10	1
Neotragus moschatus	BR	1, 1, 1	FR	3.7 ± 0.2	9.2 ± 1.5	0	8
Odocoileus virginianus	BR	1, 1, 0	FR	66.1 ± 27.6	94.4 ± 24.6	9	1
Oryx gazella	GR	1, 0, 0	FR	192.1	461.0	82	2
Oryx leucoryx	GR	0, 1, 0	Z	75.0	228.0	75	3
Ourebia ourebi	GR	0, 1, 0	FR	20.0	37.5	49	2
Ovis ammon domesticus	GR	0, 0, 1	Z	32.0	80.0	50	1
Ovis ammon musimon	GR	1, 0, 0	SFR	55.0	143.2	69	16
Pelea capreolus	BR	2, 0, 0	FR	16.3 ± 1.8	31.8 ± 2.3	7	17
Raphicerus campestris	BR	0, 0, 1	FR	10.7	15.3	10	1
Raphicerus melanotis	IM	1, 0, 0	FR	9.1	16.5	30	3
Redunca redunca	GR	0, 1, 0	FR	21.9	54.0	80	1
Rupicapra rupicapra	IM	2, 3, 0	FR	24.3 ± 7.4	58.9 ± 4.0	74	1
Sylvicapra grimmia	BR	1, 0, 0	FR	13.0	30.3	5	2
Syncerus caffer	GR	1, 0, 0	FR	650.0	1308.0	90	1
Tragelaphus angasi	BR	2, 3, 0	FR/Z	75.9 ± 38.3	147.6 ± 71.3	20	18
Tragelaphus imberbis	BR	2, 0, 0	Z	46.5 ± 5.0	94.0 ± 18.9	10	2

Table 1 continued

Species		*n* (M, F, UK)	Origin	Body mass (kg)	Masseter mass (g)	%Grass	Source[b]
Tragelaphus spekii	BR	2, 0, 0	Z	55.0 ± 9.9	101.3 ± 37.1	68	19
Tragelaphus strepsiceros	BR	1, 1, 0	FR/Z	127.5 ± 88.4	238.5 ± 139.3	5	1
Tragulus javanicus[c]	BR	2, 1, 0	FR	1.3 ± 0.1	3.8 ± 0.9	0	20
Tragulus napu[c]	BR	0, 2, 0	Z	2.7 ± 0.2	6.1 ± 0.9	0	20

[a] Diets of animals measured for this study were generally not recorded. FR animals may be assumed to have foraged naturally; SFR animals were kept on extensive pastures at Whipsnade Wild Animal Park, UK; diets of Z animals were not recorded except for *A. nasomaculatus* (grass hay, wheat bran), *B. javanicus* (fresh grass, grass hay, beet pulp), *G. subgutturosa* (fresh grass, grass hay, pelleted mixed feed, vegetables), *G. camelopardalis* (lucerne hay, browse, pelleted mixed feed, vegetables), *O. leucoryx* (grass hay, pelleted mixed feed, vegetables)

[b] Literature sources for percent grass: 1 (Van Wieren 1996), 2 (Owen-Smith 1997), 3 (Gagnon and Chew 2000), 4 (Bigalke 1972), 5 (Dhungel and O'Gara 1991), 6 (Andanje and Ottichilo 1999), 7 (Dubost 1984), 8 (Heinichen 1972), 9 (Du Plessis 1972), 10 (Geist 1999), 11 (Heptner et al. 1989), 12 (Grobler 1974), 14 (Hofmann and Stewart 1972), 15 (Branan et al. 1985), 16 (Stubbe 1971), 17 (Ferreira and Bigalke 1987), 18 (Lobao Tello and van Gelder 1975), 19 (Owen 1970), 20 (Nordin 1978); *Est.* estimated as in Clauss et al. (2006)

[c] Data from Endo et al. (2002)

was performed for both a set of phylogenetic trees involving branch lengths (tree 1) and another set with equal branch lengths (tree 2). As there were no relevant differences in the results, only the tests using tree 1 are given here. In order to visualize the correlation between %grass and masseter mass after body mass had been controlled for, the residuals of the masseter measurements were plotted against %grass. The residuals were calculated using allometric regression with body mass according to the equation ln (masseter muscle mass) = $a + b$ ln (BM) and served just for the purpose of demonstrating the relationship in two dimensions. The COMPARE 4.6 program (Martins 2004) served for the phylogenetically controlled calculations. The other statistical calculations were performed with the SPSS 12.0 software (SPSS, Chicago, Ill.). The significance level was set to $\alpha = 0.05$.

Results

Averaged across all species, masseter mass represented 0.212% of the body mass, with a median of 0.206 and a range of 0.128–0.313 (95% confidence interval for the mean 0.201–0.223). In general, the masseter muscle mass scaled nearly isometrically to body mass. The regression between masseter mass and body mass according to the equation, ln(masseter muscle mass) = $a + b$ ln (BM), was highly significant (without phylogeny, $R^2 = 0.983$, $P < 0.001$; including phylogeny, $R^2 = 0.983$, $P = 0.001$), and an isometric scaling in the equivalent power equation, masseter muscle mass = e^a BM^b (exponent $b = 1.0$), was just excluded by the 95% confidence interval (without phylogeny, 0.925–0.999; including phylogeny, 0.921–0.996).

The relationship between BM and the mass of the masseter muscle differed among the three categorial feeding types (Fig. 2). The slopes of the regression lines for BR, IM, and GR differed ($P = 0.038$). When IM were excluded, slopes for BR and GR did not differ significantly ($P = 0.592$), and both significant effects of body mass ($P < 0.001$) and feeding type occurred (i.e. a significant difference between BR and GR, $P < 0.001$). When the three categorical feeding types were compared including phylogeny, there was also a significant difference in slopes ($P = 0.049$). After excluding the IM, there was no significant difference between the slopes ($P = 0.539$), and again, both body mass ($P < 0.001$) and feeding type (i.e. BR vs. GR, $P < 0.001$) showed significant effects.

Regardless of whether phylogeny was accounted for or not, both body mass (Fig. 2) and %grass in the natural diet (Fig. 3) showed a significant, positive correlation to the masseter muscle mass according to the equation, ln (masseter muscle mass) = $a + b$ ln (BM) + c %grass [without phylogeny, $R^2 = 0.987$, $P(R^2) < 0.001$, $a = 0.892$, $b = 0.922$, $P(b) < 0.001$, $c = 0.003$, $P(c) < 0.001$; including phylogeny, $R^2 = 0.986$, $P(R^2) < 0.001$, $a = 0.882$, $b = 0.926$, $P(b) < 0.001$, $c = 0.003$, $P(c) = 0.003$].

Discussion

Using the traditional, categorical feeding types, we found a significant difference in masseter mass between grazing and browsing ruminants that was independent of body mass and phylogeny. Differences in slopes have been encountered repeatedly in comparisons of categorical feeding types (see Table 3.5 in Clauss et al. 2008); the use of a continuous variable such as %grass prevents this problem and allowed, in this case, the use of the full dataset of 48 species to corroborate the result. In preparing categorical tests, the classification of individual ruminant species into feeding types is problematic, because no standardized cut-off points exist for the transitions between intermediate feeders and the two extreme feeding types. This problem had already been

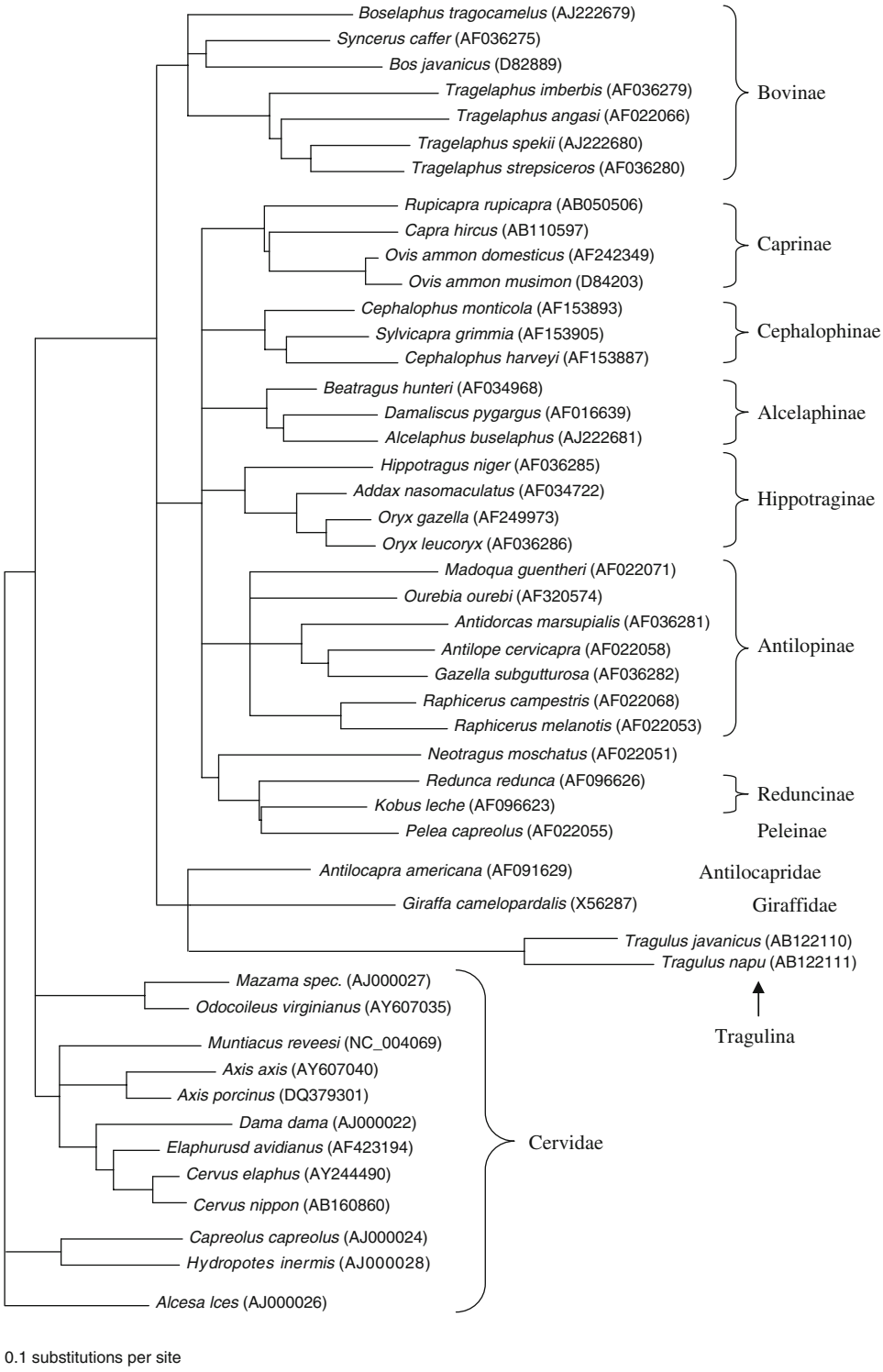

Fig. 1 Fifty percent majority rule maximum likelihood tree (100,000 puzzling steps, log $L = -188{,}62.584$), depicting the phylogenetic relationships among complete mitochondrial cytochrome *b* sequences from 48 ruminant taxa as used in the phylogenetically controlled statistics in this study (accession codes from GenBank (http://www.ncbi.nlm.nih.gov)

indicated by Gordon and Illius (1994) who found evidence supporting the hypotheses of Hofmann (1989) when using Hofmann's own categorical classification but could not support these hypotheses with a classification of their own. Actually, the practice of grouping species into feeding type categories has not been consistent even within research groups over time (discussed in Clauss et al. 2008). Therefore, the use of quantitative data on the proportion of grass in the natural diet, rather than a categorical classification, has been proposed as a more suitable alternative (Janis 1995; Clauss et al. 2003, 2006; Sponheimer et al. 2003; Pérez-Barbería et al. 2004; Pérez-Barbería and Gordon 2005; Codron et al. 2007b; Hofmann et al. 2008). In our analysis here, we found that the mass of the masseter

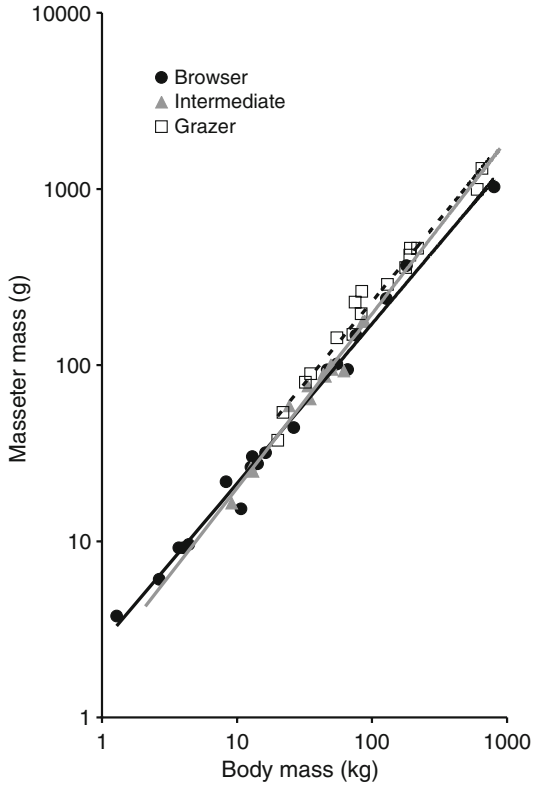

Fig. 2 Relationship between body mass and masseter muscle mass in 48 ruminant species (from Table 1) classified into three distinct feeding types. Slopes were similar for browsers (*solid black line*) and grazers (*dotted line*) but not for intermediate feeders (*solid grey line*)

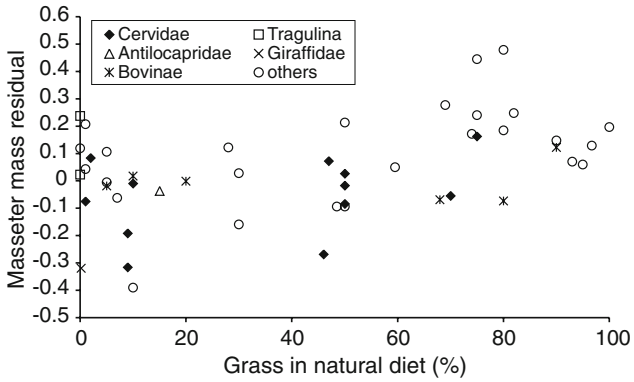

Fig. 3 Relationship of the phylogeny-controlled body mass residuals of the masseter muscle mass with the percentage of grass in the natural diet of ruminant species

muscle increased with the estimated proportion of grass in the natural diet, when controlling for body size and phylogeny.

However, getting reliable estimates of the species-specific proportion of grass in the natural diet is not an easy task (Clauss et al. 2008). Such data mostly come from collations using a variety of methods and are from studies of varying reliability (Gagnon and Chew 2000); variations due to seasonality and locality are not taken into account; and the data on the composition of the natural diet are mostly not taken directly from the population from which the individuals measured derived (but see Codron et al. 2008b). Therefore, any analysis combining datasets of different origin must be treated with appropriate caution.

Hendrichs (1965) demonstrated that the mass of the masticatory muscles represented more than 300% of the mass of the mandibles in carnivores but only about 240% in nonruminant herbivores, with the evident conclusion that the cutting, tearing and mastication of flesh and bones requires stronger forces than that of plant material. For ruminant herbivores, this ratio was even lower at 130%. Although empirical data are lacking, it is generally assumed that in comparison to nonruminant herbivores, rumination "relaxes" the functional load on the masticatory apparatus, because a part of the masticatory activity is performed on material that has already been soaked in ruminal fluid and "softened" by ruminal fermentation processes (Fortelius 1985; Sanson 1989). Taking these differences between major animal groups as indicators of differences in function, we can also hypothesize that differences in masticatory muscle mass within one of these groups—the ruminants—does have functional relevance.

In ruminants, the masseter is the largest of the masticatory muscles, representing between 44 and 54% of the total weight of all masticatory muscles combined (Hendrichs 1965). Changes in masseter muscle mass should therefore have a distinct influence on the masticatory processes in a ruminant organism. Given the equation described in the results, we can calculate a theoretical difference between a species consuming 10% of grass and a species consuming 90% of grass in their natural diets to be 11, 25, 48, 91, 213 or 405 g at body masses of 20, 50, 100, 200, 500 or 1,000 kg, respectively. At any given body mass, a theoretical browser (10% grass) would have, according to the equation, approximately 80% of the masseter muscle mass of a theoretical grazer (90% grass). These differences appear to be large enough to result in actual differences in masticatory forces applied.

Experimental studies have shown that differences in resistance to chewing actually do exist between some forage classes. Trials in agricultural science indicated that legumes are less costly to diminish in particle size than grasses when tested mechanically (Paul and Mika 1981; unpublished data in Wilson and Kennedy 1996; Henry et al. 1997; Wilman et al. 1997) or in vivo by the mastication action of domestic ruminants (Moseley and Jones 1984; Waghorn et al. 1989; Wilman et al. 1997). This is also reflected in the longer time spent ruminating (per unit of forage intake) for grass as compared with legumes in domestic ruminants (Sudweeks et al. 1981; Wilman et al. 1997; data in Coleman et al. 2003). If a closer similarity is assumed between leguminous forages fed to domestic ruminants on the one hand, and browse material

ingested by free-ranging, browsing ruminants on the other hand (as opposed to grass forage), then these reports support the general concept of grazers needing a particularly strong masticatory apparatus. Van Soest (1994, p. 54) speculated correspondingly that free-ranging, grazing wild ruminants spend a higher proportion of their activity budget ruminating than browsing ruminants, but the available data allowed no convincing conclusion. The only systematic comparison of forage classes with respect to their physical "resistance" is the investigation of Cornelissen and Thompson (1997) on litter decomposition rates and their factors of influence. These authors demonstrated that graminoid monocots had a drastically higher leaf tensile strength, or tearing resistance, than herbaceous dicots; no other dicots were tested in that study; however, the authors cite unpublished data on unspecified tree foliage that had a tensile strength higher than the herbaceous dicots but still lower than the monocots tested.

Together with the laminar surface area of the omasum (Clauss et al. 2006) and the salivary gland mass (Hofmann et al. 2008), the masseter muscle mass represents the only soft tissue parameter for which a correlation with %grass has been demonstrated so far in statistical tests accounting for phylogenetic linkage. Additionally, Pérez-Barbería et al. (2004) showed that the capability to digest fibre was higher in captive wild ruminant species with higher %grass, independent of phylogenetic relationships. More detailed studies on the differentiation of ruminant feeding types appear as logical further steps: The relevance of dietary shifts between seasons (Codron et al. 2007a, b) needs to be investigated with respect to morphophysiological adaptations. As grinding of C4 grasses needs distinctively more force than that of C3 grasses (Caswell et al. 1973), possibly due to a greater percentage of bundle sheaths in C4 grasses (Heckathorn et al. 1999), a differential look at the grazer guild that accounts for the different grass types ingested appears warranted. Additionally, the evolutionary history of individual ruminant groups or species (Codron et al. 2008a; Hofmann et al. 2008), which might have led to different morphophysiological solutions to the same feeding niches, remains to be explored in detail.

Acknowledgements We thank the numerous hunters and zoological institutions that helped collecting material. M. C. particularly thanks Nadia Robert and Christian Wenker for the provision of giraffid material and J. C. Castell for assistance at dissections, D. Jäger for support in literature review, and B. Schneider for support in literature acquisition. Norman Owen-Smith kindly provided the data collection from his 1997 publication. We thank Atle Mysterud and one anonymous reviewer for helpful comments on previous versions of this manuscript.

References

Andanje SA, Ottichilo WK (1999) Population status and feeding habits of the translocated subpopulation of Hunter's antelope or hirola (*Beatragus hunteri*) in Tsavo East National Park, Kenya. Afr J Ecol 37:38–48

Axmacher H, Hofmann RR (1988) Morphological characteristics of the masseter muscle of 22 ruminant species. J Zool 215:463–473

Bigalke RC (1972) Observations on the behavior and feeding habits of the springbok (*Antidorcas marsupialis*). Zool Afr 7:333–359

Branan WV, Werkhoven MCM, Marchinton RL (1985) Food habits of brocket and white-tailed deer in Suriname. J Wildl Manage 49:972–976

Caswell H, Reed F, Stephenson SN, Werner PA (1973) Photosynthetic pathways and selctive herbivory: a hypothesis. Am Nat 107:465–480

Clauss M, Lechner-Doll M, Streich WJ (2003) Ruminant diversification as an adaptation to the physicomechanical characteristics of forage. A reevaluation of an old debate and a new hypothesis. Oikos 102:253–262

Clauss M, Hofmann RR, Hummel J, Adamczewski J, Nygren K, Pitra C, Reese S (2006) The macroscopic anatomy of the omasum of free-ranging moose (*Alces alces*) and muskoxen (*Ovibos moschatus*) and a comparison of the omasal laminal surface area in 34 ruminant species. J Zool 270:346–358

Clauss M, Kaiser T, Hummel J (2008) The morphophysiological adaptations of browsing and grazing mammals. In: Gordon IJ, Prins HHT (eds) The ecology of browsing and grazing. Springer, Heidelberg, pp 47–88

Codron D, Codron J, Lee-Thorp JA, Sponheimer M, de Ruiter D, Sealy J, Grant R, Fourie N (2007a) Diets of savanna ungulates from stable carbon isotope composition of faeces. J Zool 273:21–29

Codron D, Lee-Thorp JA, Sponheimer M, Codron J, de Ruiter D, Brink JS (2007b) Significance of diet type and diet quality for ecological diversity of African ungulates. J Anim Ecol 76:526–537

Codron D, Brink JS, Rossouw L, Clauss M (2008a) The evolution of ecological specialization in southern African ungulates: competition or physical environmental turnover? Oikos 117:344–353

Codron D, Brink JS, Rossouw L, Clauss M, Codron J, Lee-Thorp JA, Sponheimer M (2008b) Functional differentiation of African grazing ruminants: an example of specialized adaptations to very small changes in diet. Biol J Linn Soc (in press)

Coleman SW, Hart SP, Sahlu T (2003) Relationships among forage chemistry, rumination and retention time with intake and digestibility of hay by goats. Small Ruminant Res 50

Cornelissen JHC, Thompson K (1997) Functiona leaf attributes predict litter decomposition rate in herbacous plants. New Phytol 135:109–114

Dhungel SK, O'Gara BW (1991) Ecology of the hog deer in Royal Chitwan National Park, Nepal. Wildl Monogr 119:1–40

Du Plessis SS (1972) Ecology of blesbok with special reference to productivity. Wildl Monogr 30:1–70

Dubost G (1984) Comparsion of the diets of frugivorous forest ruminants of Gabon. J Mammal 65:298–316

Endo H, Kimura J, Sasaki M, Matsuzaki M, Matsubayashi H, Tanaka K, Fukuta K (2002) Functional morphology of the mastication muscles in the lesser and greater mouse deer. J Vet Med Sci 64:901–905

Fernandez MH, Vrba ES (2005) A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. Biol Rev 80:269–302

Ferreira NA, Bigalke RC (1987) Food selection by grey rhebuck in the Orange Free State. S Afr J Wildl Res 17:123–127

Fortelius M (1985) The functional significance of wear induced change in the occlusal morphology of herbivore cheek teeth, exemplified by *Dicerorhinus etruscus* upper molars. Acta Zool Fenn 170:157–158

Gagnon M, Chew AE (2000) Dietary preferences in extant African bovidae. J Mammal 81:490–511

Geist V (1999) Deer of the world. Their evolution, behaviour, and ecology. Swan Hill Press, Shrewsbury, UK

Gordon IJ, Illius AW (1994) The functional significance of the browser-grazer dichotomy in African ruminants. Oecologia 98:167–175
Grobler JH (1974) Aspects of the biology, population ecology and behaviour of the sable (*Hippotragus niger*) in the Rhodes Matopos National Park, Rhodesia. Arnold Rhod 7:1–36
Heckathorn SA, McNaughton SJ, Coleman JS (1999) C4 plants and herbivory. In: Sage RF, Monson RK (eds) C4 plant biology. Academic Press, San Diego, pp 285–312
Heinichen IG (1972) Preliminary notes on the suni (*Neotragus moschatus*) and the red duiker (*Cephalophus natalensis*). Zool Afr 7:157–165
Hendrichs H (1965) Vergleichende Untersuchung des Wiederkauverhaltens. Biol Zent Bl 84:681–751
Henry DA, Simpson RJ, Macmillan RH (1997) Intrinsic shear strngth of leaves of pasture grasses. Aust J Agric Res 48:667–674
Heptner VG, Nasimowitsch AA, Bannikov AG (1989) Mammals of the Sowiet Union, vol 1. Brill, Leiden
Hofmann RR (1988) Morphophysiological evolutionary adaptations of the ruminant digestive system. In: Dobson A, Dobson MJ (eds) Aspects of digestive physiology in ruminants. Cornell University Press, Ithaca, pp 1–20
Hofmann RR (1989) Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443–457
Hofmann RR (1991) Endangered tropical herbivores—their nutritional requirements and habitat demands. In: Ho YW, Wong HK, Abdullah N, Tajuddin ZA (eds) Recent advances on the nutrition of herbivores. Malaysia Society of Animal Production. UPM, Serdang, pp 27–34
Hofmann RR, Stewart DRM (1972) Grazer or browser: a classification based on the stomach-structure and feeding habit of East African ruminants. Mammalia 36:226–240
Hofmann RR, Knight MH, Skinner JD (1995) On structural characteristics and morphophysiological adaptation of the springbok (*Antidorcas marsupialis*) digestive system. Trans R Soc S Afr 50:125–142
Hofmann RR (1999) Functional and comparative digestive system anatomy of Arctic ungulates. Rangifer 20:71–81
Hofmann RR, Streich WJ, Fickel J, Hummel J, Clauss M (2008) Convergent evolution in feeding types: salivary gland mass differences in wild ruminant species. J Morphol 269:240–257
Janis CM (1990) Correlation of cranial and dental variables with dietary preferences in mammals: a comparison of macropidoids and ungulates. Mem Queensl Mus 28:349–366
Janis CM (1995) Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. In: Thomason JJ (ed) Functional morphology in vertebrate paleontology. Cambridge University Press, New York, pp 76–98
Kiplel MN (1981) The topography and functional anatomy of the masticatory muscles in seven ruminant species of the intermediate feeding type. MSc thesis, University of Nairobi
Lanave C, Preparata G, Sacone C, Serio G (1984) A new method for calculating evolutionary substitution rates. J Mol Evol 20:86–93
Lobao Tello JL, van Gelder RG (1975) The natural history of nyala (*Tragelaphus angasi*) in Mozambique. Bull Am Mus Nat His 155:319–386
Martins E (2004) COMPARE, version 4.6. Computer programs for the statistical analysis of comparative data. Distributed by the author at http://www.compare.bio.indiana.edu/. Department of Biology, Indiana University, Bloomington
Martins E, Hansen T (1997) Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into analysis of interspecific data. Am Nat 149:646–667
Mendoza M, Palmqvist P (2006) Characterizing adaptive morphological patterns related to diet in bovidae. Acta Zool Sin (in press)
Mendoza M, Janis CM, Palmqvist P (2002) Characterizing complex craniodental patterns related to feeding behaviour in ungulates: a multivariate approach. J Zool 258:223–246
Moseley G, Jones JR (1984) The physical digestion of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) in the foregut of sheep. Br J Nutr 52:381–390
Nakamura YN, Iwamoto H, Etoh T, Shiotsuka Y, Yamaguchi T, Ono Y, Tabata S, Nishimura S, Gotoh T (2007) Three-dimensional observation of connective tissue of bovine masseter muscle under concentrate- and roughage-fed conditions by using immunohistochemical/confocal laser-scanning microscopic methods. J Food Sci 72:E375–E381
Nordin M (1978) Voluntary food intake and digestion by the lesser mousedeer. J Wildl Manage 42:185–186
Owen REA (1970) Some observations on the sitatunga in Kenya. East Afr Wildl J 8:181–195
Owen-Smith N (1997) Distinctive features of the nutritional ecology of browsing versus grazing ruminants. Z Säugetierkd 62(Suppl 2):176–191
Paul C, Mika V (1981) Mahlwiderstandsmessungen an Rauhfutter. II. Beziehungen zwischen Mahlwiderstand und Futterwertmerkmalen. Landbauforschung Völkenrode 31:163–169
Pérez-Barbería FJ, Gordon IJ (2005) Gregariousness increases brain size in ungulates. Oecologia 145:41–52
Pérez-Barbería FJ, Gordon IJ, Illius A (2001) Phylogenetic analysis of stomach adaptation in digestive strategies in African ruminants. Oecologia 129:498–508
Pérez-Barbería FJ, Elston DA, Gordon IJ, Illius AW (2004) The evolution of phylogenetic differences in the efficiency of digestion in ruminants. Proc R Soc Lond B 271:1081–1090
Pitra C, Fickel J, Meijaard E, Groves PC (2004) Evolution and phylogeny of old world deer. Mol Phylogenet Evol 33:880–895
Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818
Purvis A, Garland T (1993) Polytomies in comparative analyses of continous characters. Syst Biol 42:569–575
Ramisch W (1978) Topographie und funktionelle Anatomie der Kaumuskeln und der Speicheldrüsen des Rehes (Capreolus capreolus). Dissertation thesis, University of Giessen
Rodriguez F, Oliver JF, Marin A, Medina JR (1990) The general stochastic model of nucleotide substitution. J Theor Biol 142:485–501
Rohlf F (2001) Comparative methods for the analysis of continuous variables: geometric interpretations. Evolution 55:2143–2160
Sanson GD (1989) Morphological adaptations of teeth to diets and feeding in the macropodoidea. In: Grigg G, Jarman P, Hume I (eds) Kangaroos, wallabies and rat-kangaroos. Surrey-Beatty, Sydney, pp 151–168
Sasaki M, Endo H, Kogiku H, Kitamura N, Yamada J, Yamamoto M, Arishima K, Hayashi Y (2001) The structure of the masseter muscle in the giraffe (*Giraffa camelopardalis*). Anat Histol Embryol 30:313–319
Schmidt HA, Strimmer K, Vingron M, von Haeseler A (2002) TREE-PUZZLE: maximum likelihood phylogenetic analysis using quartets and parallel computing. Bioinformatics 18:502–504
Solounias N, Dawson-Saunders B (1988) Dietary adaptations and palaecology of the late Miocene ruminants from Pikermi and Samos in Greece. Palaeogeogr Palaeoclimatol Palaeoecol 65:149–172
Solounias N, Moelleken SMC (1999) Dietary determination of extinct bovids through cranial foraminal analysis, with radiographic applications. Ann Mus Goulandris 10:267–290
Solounias N, Moelleken S, Plavcan J (1995) Predicting the diet of extinct bovids using masseteric morphology. J Vertebr Paleontol 15:795–805
Sponheimer M, Lee-Thorp JA, DeRuiter D, Smith JM, Van der Merwe NJ, Reed K, Grant CC, Ayliffe LK, Robinson TF, Heidelberger C,

Marcus W (2003) Diets of Southern African bovidae: stable isotope evidence. J Mammal 84:471–479

Stöckmann W (1979) Differences in the shape of the mandibles of African bovidae in relation to food composition. Zool Jahrbüch Syst 106:344–373

Stubbe C (1971) Zur Ernährung des Muffelwildes (*Ovis ammon musimon*) in der DDR. Beitr Jagd Wildforschung 7:103–125

Sudweeks EM, Ely LO, Mertens DR, Sisk LR (1981) Assessing minimum amounts and form of roughages in ruminant diets: roughage value index system. J Anim Sci 53:1406–1411

Swofford DL (2002) PAUP*: phylogenetic analyses using parsimony (and other methods), version 4.0 beta. Smithsonian Institition, Washington DC

Tavaré S (1986) Some probabilistic and statistical problems in the analysis of DNA sequences. Lect Math Life Sci 17:57–86

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 15:4876–4882

Turnbull WD (1970) Mammalian masticatory apparatus. Fieldiana. Geology 18:147–356

Van Soest PJ (1994) Nutritional ecology of the ruminant. Cornell University Press, Ithaca

Van Wieren SE (1996) Browsers and grazers: foraging strategies in ruminants. In: Van Wieren SE (ed) Digestive strategies in ruminants and nonruminants. Thesis landbouw. University of Wageningen, Wageningen, pp 119–146

Waghorn GC, Shelton ID, Thomas VJ (1989) Particle breakdown and rumen digestion of fresh ryegrass (*Lolium perenne*) and lucerne (*Medicago sativa*) fed to cows during a restricted feeding period. Br J Nutr 61:409–423

Wilman D, Derrick RW, Moseley G (1997) Physical breakdown of chickweed, dandelion, dock, ribwort, spurrey and perennial ryegrass when eaten by sheep and when macerated. J Agric Sci 129:419–428

Wilson JR, Kennedy PM (1996) Plant and animal constraints to voluntary feed intake associated with fibre characteristics and particle breakdown and passage in ruminants. Aust J Agric Res 47:199–125